BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 10 JULY 2013 NUMBER 535

BEHAVIORAL PARTITIONING BY THE NATIVE LIZARD *ANOLIS CAROLINENSIS* IN THE PRESENCE AND ABSENCE OF THE INVASIVE *ANOLIS SAGREI* IN FLORIDA

AMBIKA KAMATH,[1] YOEL E. STUART,[1] AND TODD S. CAMPBELL[2]

ABSTRACT. Animals are known to engage in different behaviors in different parts of their home range, and the overall habitat occupied by an individual influences where it engages in particular behaviors. However, few studies have investigated how changes in habitat use alter the partitioning of an animal's behaviors into different microhabitats. In eastern Florida, the native lizard *Anolis carolinensis* is known to change its habitat use in the presence of invasive *Anolis sagrei* by perching higher in the canopy. We assessed behavioral partitioning in island populations of *A. carolinensis* that are sympatric with *A. sagrei* compared with islands where *A. carolinensis* is allopatric. We found that individuals of *A. carolinensis* exhibited behavioral partitioning, feeding relatively lower and displaying relatively higher than their initial perch height in both the presence and absence of *A. sagrei*. However, the relative locations chosen for feeding and displaying were not affected by the presence of *A. sagrei*, suggesting that habitat changes need not affect behavioral partitioning.

INTRODUCTION

Many animals engage in different behaviors in different parts of their habitat, with particular microhabitats utilized for foraging (Albers and Gehlbach, 1990; Thornton and Hodge, 2009), sleeping (Anderson, 1998; Singhal *et al.*, 2007), breeding (Hagman and Shine, 2006), and nesting (Kats and Sih, 1992; Angiletta *et al.*, 2009). Such partitioning of an individual's behavioral repertoire into different microhabitats is thought to be adaptive. For instance, choosing sleeping sites with relatively low predation rates (e.g., Anderson, 1998; Clark and Gillingham, 2006) or foraging sites where the energetic returns of feeding are relatively high (e.g., Wanless *et al.*, 1998) are behaviors likely favored by selection.

The optimal locations for engaging in particular behaviors likely depend on the type of habitat occupied by a species. Within

[1] Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, U.S.A.; e-mail: akamath@fas.harvard.edu

[2] Department of Biology, University of Tampa, 401 W. Kennedy Boulevard, Tampa, Florida 33606, U.S.A.

© The President and Fellows of Harvard College 2013.

SHOUT
SHARE
IT
SECURITY

a species, habitat use often differs among populations depending on whether or not they are sympatric with closely related, ecologically similar species (e.g., Schoener, 1975; Medel *et al.*, 1988; Schluter and McPhail, 1992; Dietrich and Werner, 2003). Interspecific interactions such as resource competition, agonistic interactions, intraguild predation, and reproductive interference often have negative fitness consequences for one or both species (Polis *et al.*, 1989; Gronig and Hochkirch, 2008; Grether *et al.*, 2009; Hendry *et al.*, 2009), and changes in habitat use by species in sympatry may be favored to reduce the frequency of such interactions.

Despite the prevalence of documented habitat shifts between populations of a species that differ in whether or not they are sympatric with another species, little attention has been paid to the behavioral consequences of such shifts. *Anolis* lizards are an excellent group in which to study the effects of among-population variation in habitat use on behavioral partitioning. At least two *Anolis* species are known to engage in different behaviors at different perch heights: social interactions between male *Anolis polylepis* occur at high perch heights, and both male and female *A. polylepis* and female *Anolis distichus* scan for and capture prey at low perch heights, relative to the average perch height of the population (Andrews, 1971; Paterson, 1999). Moreover, many *Anolis* species exhibit intraspecific variation in habitat use between populations that differ in whether or not they are sympatric with another anole: the average perch height of individuals in populations sympatric with other anoles often differs from the average perch height of individuals in allopatric populations (Schoener, 1975; Jenssen, 1973; Jenssen *et al.*, 1984; Losos *et al.*, 1993; Losos and Spiller, 1999; Campbell, 2000; Kolbe *et al.*, 2008; Edwards and Lailvaux, 2012).

In this study, we first examined whether individuals of the green anole, *Anolis carolinensis*, partition their behavioral repertoire such that they engage in different behaviors at different perch heights. Based on previous examples of behavioral partitioning in anoles (Andrews, 1971; Paterson, 1999), we predicted that, relative to their initial perch heights, *A. carolinensis* would feed at low perches and display at high perches.

Second, we assessed whether behavioral partitioning in *A. carolinensis* is modified due to its perch height shift in the presence of a congeneric competitor (Collette, 1961; Campbell, 2000; Edwards and Lailvaux, 2012). *Anolis carolinensis* is the only anole native to the U.S.A. Its closest relatives are arboreal, Cuban, trunk-crown ecomorph anoles (Williams, 1969; Glor *et al.*, 2005) that partition the vertical habitat with the low-dwelling, trunk-ground anole *Anolis sagrei*, as well as with up to 10 other *Anolis* species. The absence of other anoles from the continental U.S.A. has enabled the expansion of *A. carolinensis*' habitat to include a wider range of perch heights—an example of ecological release (Collette, 1961; Losos, 2009). However, the invasion of *A. sagrei* into the U.S.A., where it is now broadly sympatric with *A. carolinensis* in Florida, has led *A. carolinensis* to shift back to higher perches (Collette, 1961; Campbell, 2000; Edwards and Lailvaux, 2012). We assessed the effect of this perch-height shift on behavioral partitioning by comparing allopatric island populations of *A. carolinensis* with island populations of *A. carolinensis* sympatric with *A. sagrei*.

MATERIALS AND METHODS

Study system

In the 1950s, the U.S. Army Corps of Engineers established 53 dredge-spoil islands in the Intracoastal Waterway along the western edge of Mosquito Lagoon in Volusia

TABLE 1. DISTANCE TO MAINLAND, PERIMETER LENGTH, AND AREA OF THE ISLANDS WITH AND WITHOUT *ANOLIS SAGREI* SAMPLED IN THIS STUDY.

Island	*A. sagrei* Presence	Distance to Mainland (m)	Perimeter Length (m)	Area (m^2)
Hornet	absent	365	349	5,601
South Twin	absent	222	557	12,956
Lizard	present	201	478	9,272
Line of Cedars	present	335	487	12,281

and Brevard Counties, Florida (Campbell and Echternacht, 2003). These islands were colonized by mainland flora and fauna, including *A. carolinensis*. *Anolis sagrei* reached Mosquito Lagoon in the late 1980s and subsequently invaded many but not all of the Lagoon's spoil islands (Campbell and Echternacht, 2003). For this study, data were collected from two islands where only *A. carolinensis* is present (hereafter one-species islands: Hornet and South Twin) and two islands with both *A. carolinensis* and *A. sagrei* (hereafter two-species islands: Lizard and Line of Cedars). Colonization by *A. sagrei* appears to be random with respect to island characteristics—islands with and without *A. sagrei* sampled in this study do not appear to differ in their distance to the mainland, area, and perimeter length (Table 1). Further, neither total tree height nor plant species composition differs between the islands with and without *A. sagrei* across Mosquito Lagoon (Y. E. Stuart, unpublished data), making it unlikely that perch availability differs between the one- and two-species islands that we sampled. Thus, any differences in *A. carolinensis* behavior between one- and two-species islands are likely due to the presence of *A. sagrei* rather than environmental differences between islands with and without *A. sagrei*.

Data collection

We conducted focal observations lasting 2–20 minutes (mean ± standard error: 15.1 ± 0.7 minutes) on undisturbed male and female lizards between 0700 and 1830 hours from 12 July to 6 August 2010. Over 98% of the observations were made between 0700 and 1400 hours. Lizards were found using the Rand census method (Rand, 1964; Losos, 2009), whereby we walked slowly through the environment until we spotted an undisturbed individual. All observations were made by a single observer (AK) and were restricted to relatively open habitats, so that a distance of at least 2 m could be maintained between the lizard and the observer. Observations lasted until the lizard disappeared from view or up to a maximum of 20 minutes. If possible, lizards were caught and marked with a nontoxic Sharpie® marker after the observation period to ensure that lizards were not resampled during subsequent island visits. Captured lizards were also permanently tagged with nontoxic VI Alpha Tags (Northwest Marine Technology, Inc.) to further reduce the possibility of resampling. Finally, lizards were also caught on these islands for a different study (Y. E. Stuart, unpublished data), enabling us to set a lower bound on the number of lizards present on these islands; our mean sample size per island (9.6 ± 1.2) was substantially lower than the mean minimum number of lizards present per island (93.5 ± 7.0), making it unlikely that we resampled individuals during our study.

After each observation period, we measured initial lizard perch height (i.e., the height above the ground in centimeters where the lizard was first observed) as well

as lizard perch height at all observed feeding locations. We also noted perch heights for displaying lizards (including both head bobbing and dewlap extensions; Jenssen, 1977, 1978) if they displayed at their initial perch, and measured perch heights for any displays following upward or downward vertical movements of 10 cm or more. This method is equally likely to detect displays that occur above, below, or at the same height as the initial perch, and given our directional prediction that displays will occur at relatively high perches, data collected by this method are not biased toward confirming our expectations. Display heights were analyzed only for males because displaying is a significant component of the behavioral repertoire of male but not female *A. carolinensis* in the breeding season (Jenssen *et al.*, 1995; Nunez *et al.*, 1997), and, indeed, only three females were observed displaying across the four islands. These perch-height measurements enabled the comparison of initial perch height, perch height at feeding events, and, for males, perch height at displaying events across islands. Our comparison of feeding or displaying perch heights with initial perch height is based on the widely held but rarely mentioned assumption that the average initial perch height approximates the average perch height of individuals in a population (Rand, 1964).

Statistical analyses

To test whether feeding height was consistently lower than initial perch height across all islands, we combined independent one-tailed *P*-values from four within-island paired *t* tests of initial perch height against feeding height, using the weighted *Z* method for combining probabilities (Whitlock, 2005) to generate a single one-tailed *P*-value for the comparison. One-tailed tests were justified by our directional predictions that, relative to their initial perch heights, *A. carolinensis* would feed at low perches. If an individual lizard fed multiple times within an observation, the mean feeding height for that individual was calculated and used in all analyses. Mean differences between initial perch height and feeding height were similar for males and females (mean difference ± standard error for males [$n = 13$]: 15.7 ± 11.6 cm; females [$n = 22$]: 16.9 ± 4.9 cm); hence we pooled both sexes for analyses of differences between feeding height and initial height. We similarly tested whether, for males, display height was consistently higher than initial perch height across all islands.

We confirmed that lizards perched higher on two-species islands than on one-species islands using a nested analysis of variance (ANOVA), with island nested within *A. sagrei* presence, to compare initial perch height between one- and two-species islands. To examine whether microhabitat use during feeding differed between one- and two-species islands, we used a nested ANOVA, with island nested within *A. sagrei* presence, to compare the distance by which individuals descended to feed (i.e., the difference between initial perch height and feeding height) between one- and two-species islands. Similar analyses were performed to compare the distance by which males ascended to display (i.e., the difference between display height and initial perch height) between one- and two-species islands.

All statistical analyses were carried out in JMP v. 5.0.1 (SAS Institute Inc., Cary, North Carolina 1989–2007), except the weighted *Z*-method for combining probabilities, which was implemented using the survcomp package v 1.2.1 (Schröder *et al.*, 2011) installed in R v 2.13.1 (R Development Core Team, 2011). Nested ANOVAs were performed by hand. All perch-height measurements were square-root transformed to improve normality.

RESULTS

We measured perch height at feeding for an average of 8.8 ± 1.4 individuals per island, and perch height at displaying for an average of 9.5 ± 1.9 males per island. On combining *P*-values from independent *t* tests from the four islands using the weighted *Z* method, we found that feeding height was significantly lower than initial perch height ($Z = 2.65$, $P = 0.004$; Fig. 1a). Display height was significantly higher than initial perch height ($Z = 2.24$, $P = 0.012$; Fig. 1b).

The initial perch height of *A. carolinensis* was higher in the presence of *A. sagrei* ($F_{1,2} = 92.3$, $P = 0.01$). However, the distance by which individuals descended to feed did not differ between one- and two-species islands ($F_{1,2} = 0.09$, $P = 0.79$), nor did the distance by which males ascended to display differ between one- and two-species islands ($F_{1,2} = 1.55$, $P = 0.34$).

DISCUSSION

Feeding heights

Combining *t* tests across all islands, we found that, relative to their initial perch height, individuals of *A. carolinensis* fed at lower perches. Similar partitioning by behavior of the vertical extent of the habitat is seen in *A. polylepis* (Andrews, 1971) and female *A. distichus* (Paterson, 1999), but neither the prevalence of this phenomenon across anoles nor its causes has been established. One explanation for individuals shifting lower to feed is that prey are more abundant close to the ground. Data from islands in the Intracoastal Waterway similar to those sampled in this study show that arthropod densities are highest close to ground (Campbell, 2000), and the vertical stratification of arthropod density has been documented in other systems (Lawton, 1983; Brown *et al.*, 1997). Moreover, a study on *Anolis nebulosus* has shown that individuals shift the microhabitat in which they feed based on seasonal variation in prey abundance (Lister and Aguayo, 1992). It is hence likely that anoles choose their foraging locations based on spatial variation in prey density.

Consistent with previous studies (Campbell, 2000; Edwards and Lailvaux, 2012), *A. carolinensis* perched higher on two-species islands than on one-species islands. However, the average distance that individuals of *A. carolinensis* descended to feed did not differ between one- and two-species islands. Our result would suggest that *A. carolinensis* feeds at higher perches in the presence of *A. sagrei*, which is confirmed by a direct comparison of feeding heights between treatments (nested ANOVA on feeding height, with the island effect nested within the treatment effect; treatment effect: $F_{1,2} = 10.4$, $P_{\text{one-tailed}} = 0.042$). This shift is potentially a consequence of the depletion of prey at lower perches by *A. sagrei*. Microhabitat shifts in sympatry are often accompanied by reduced overlap in diet (e.g., Huey *et al.*, 1974; Schluter and McPhail, 1992). Gut content analysis from nearby islands in the Intracoastal Waterway showed that, on two-species islands where *A. carolinensis* perches higher than *A. sagrei*, *A. carolinensis* was more likely to eat flying prey, whereas *A. sagrei* was more likely to feed on terrestrial prey (Campbell, 2000). Similarly, the higher-perching *Anolis angusticeps* and *Anolis smaragdinus* were more likely to eat flying prey than the lower-perching *A. distichus* or *A. sagrei* when these species were in sympatry (Schoener 1968), and male *A. polylepis* both perched higher and ate more arboreal prey than females (Perry, 1996). The shift in the feeding height of *A. carolinensis* between one- and two-species islands might therefore lead to intraspecific variation in diet and diet-related morphological

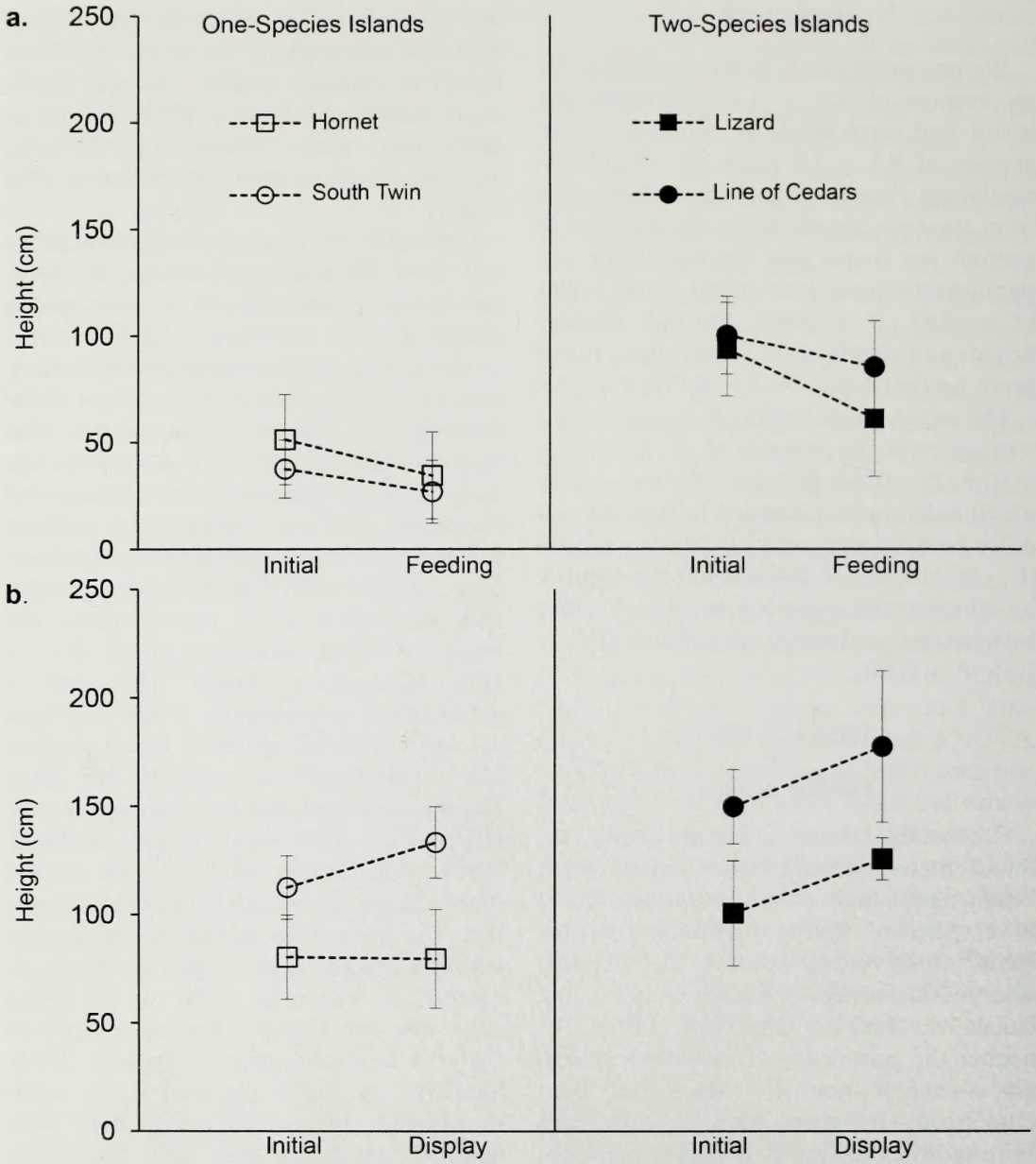

Figure 1. Comparisons of island means of (a) initial perch height and feeding height, and (b) initial perch height and display height for one-species islands (left) and two-species islands (right). Error bars indicate ±1 standard error. Note that mean initial perch heights differ between (a) and (b) because different individuals were included in each data set; only individuals observed feeding were included in the computation of mean initial perch height for the former comparison, and only males observed displaying were included in the latter.

characters of *A. carolinensis* between sympatric and allopatric populations.

Although this shift to feeding at higher perches in sympatry is potentially explained by the consequences of resource competition for food, it might also result from direct agonistic interactions between the two species if *A. carolinensis* shifts to feed at higher perches to avoid potentially costly interactions with *A. sagrei.* These selective pressures are difficult to distinguish from each other and often act simultaneously (reviewed in Grether *et al.*, 2009). Though interspecific resource competition is widely thought to drive character displacement and diversification in *Anolis* (reviewed in Losos, 2009), sympatric anoles sometimes interact aggressively (Jenssen *et al.*, 1984; Hess and Losos, 1991), and the role of agonistic interactions in driving behavioral shifts in sympatry (e.g., Ord and Martins, 2006) cannot be ruled out.

Display heights

Combining *t* tests across all islands, we found that display heights were significantly higher than initial perch heights. Andrews (1971) observed similar behavioral partitioning in *A. polylepis* and proposed that displaying from higher perches increases the conspicuousness of the displaying male to conspecific males and females. Factors such as the light environment and movement of background vegetation are known to influence where a lizard chooses to display (Leal and Fleishmann, 2002, 2004; Ord *et al.*, 2007), and might play a role in determining the visibility of an individual displaying from relatively high perches to conspecifics, congeners, or predators. Studies of territorial behavior in *Anolis* do not typically measure the vertical extent of territories (e.g., Fleming and Hooker, 1975; Stamps and Crews, 1976; Johnson *et al.*, 2009; but see Reagan, 1992; Jenssen *et al.*, 1995; Jenssen and Nunez, 1998). If relatively high perches within a territory are required by anoles for effective displaying to conspecifics, then the vertical extent of a territory might be a crucial indicator of male fitness.

The difference between initial perch height and display height is similar on both one- and two-species islands. One explanation is that display perches are chosen relative to conspecifics, irrespective of the presence of *A. sagrei.* Given the overall shift to higher perches in the presence of *A. sagrei,* this explanation implies that *A. carolinensis* males on two-species islands will be limited by their display behavior to taller trees. Indeed, *A. carolinensis* males on two-species islands are found on taller trees than individuals on one-species islands, even though the distribution of tree heights does not differ across island types (mean ± standard error of total height of trees utilized by lizards on one-species islands: 305.3 ± 7.4 cm; two-species islands: 386.2 ± 6.1cm; Y. E. Stuart, unpublished data). Shifts in the horizontal spatial distribution of *A. carolinensis* to taller trees in the presence of *A. sagrei* might therefore be mediated by a constraint on male display height relative to the perch height of conspecifics.

It is possible that, by observing lizards from eye level, we failed to observe displays that occurred at higher perches. In particular, such a detection method might prevent us from uncovering a larger difference between initial and display heights on two-species islands than on one-species islands. However, our conclusions about the shift of *A. carolinensis* males on two-species islands to taller trees due to higher display perches would remain unchanged. Given that initial perch heights and feeding heights are lower than display heights (Fig. 1), this detection bias is unlikely to alter our other conclusions, unless initial perch heights or feeding heights are bimodally distributed.

Conclusion

The partitioning of an individual's behavioral repertoire into different parts of its habitat is common in animals (e.g., Albers and Gehlbach, 1990; Kats and Sih, 1992; Hagman and Shine, 2006; Angiletta *et al.*, 2009; Thornton and Hodge, 2009) and has previously been documented in two species of *Anolis* lizards (*A. polylepis*, Andrews, 1971; *A. distichus*, Paterson, 1999). In this study, we show that individuals of *A. carolinensis* also partitioned behaviors by feeding and displaying at different heights relative to their initial perch position. Moreover, though the presence of the congeneric competitor, *A. sagrei*, has caused an overall shift to higher perches in *A. carolinensis* (Campbell, 2000; Edwards and Lailvaux, 2012; this study), the relative positions of feeding and displaying locations were not affected by the presence of *A. sagrei*. The functional reasons for behavioral partitioning as well as the mechanisms leading to overall habitat shifts in sympatry will need to be established before we can understand whether and how behavioral partitioning can vary as habitat use changes.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ACKNOWLEDGMENTS

We thank M. Legare and J. Lyon at Merritt Island National Wildlife Refuge (U.S. Fish and Wildlife Service permit: 2009-SUP-027) and J. Stiner and C. Carter at Canaveral National Seashore (National Park Service permit: CANA-2009-SCI-0006) for their gracious help with permits and logistics. The experiments were in accordance with Harvard University Institutional Animal Care and Use Committee Protocol 26-11. J. McCrae generously lent us his boat to access the islands. We thank J. Losos, G. Gartner, M. Muñoz, and the Losos Lab, as well as several anonymous reviewers for comments that improved the manuscript. AK was supported by the Amherst College Schupf Scholars Program and YES by a Museum of Comparative Zoology Miyata Award.

LITERATURE CITED

Albers, R. P., and F. R. Gehlbach. 1990. Choices of feeding habitat by relict Montezuma quail in central Texas. *Wilson Bulletin* **102:** 300–308.

Anderson, J. R. 1998. Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *American Journal of Primatology* **46:** 63–75.

Andrews, R. M. 1971. Structural habitat and time budget of a tropical *Anolis* lizard. *Ecology* **52:** 262–270.

Angiletta, M. J., M. W. Sears, and R. M. Pringle. 2009. Spatial dynamics of nesting behavior: lizards shift microhabitats to construct nests with beneficial thermal properties. *Ecology* **90:** 2933–2939.

Brown, J. L., S. Vargo, E. F. Connor, and M. S. Nuckols. 1997. Causes of vertical stratification in the density of *Cameraria hamadryadella*. *Ecological Entomology* **22:** 16–25.

Campbell, T. S. 2000. Analyses of the effects of an exotic lizard (*Anolis sagrei*) on a native lizard (*Anolis carolinensis*) in Florida, using islands as experimental units. Unpublished Ph.D. Dissertation. Knoxville, Tennessee, University of Tennessee.

Campbell, T. S., and A. C. Echternacht. 2003. Introduced species and moving targets: changes in body sizes of introduced lizards following experimental introductions and historical invasions. *Biological Invasions* **5:** 193–212.

Clark, D. L., and J. C. Gillingham. 2006. Sleep-site fidelity in two Puerto Rican Lizards. *Animal Behaviour* **39:** 1138–1148.

Collette, B. B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba, and southern Florida. *Bulletin of the Musuem of Comparative Zoology* **125:** 137–162.

Dietrich, B., and R. Werner. 2003. Sympatry and allopatry in two desert ant sister species: how do *Cataglyphis bicolor* and *C. savignyi* coexist? *Oecologia* **136:** 63–72.

Edwards, J. R., and S. P. Lailvaux. 2012. Display behavior and habitat use in single and mixed populations of *Anolis carolinensis* and *Anolis sagrei* lizards. *Ethology* **118:** 494–502.

FLEMING, T. H., AND R. S. HOOKER. 1975. *Anolis cupreus*: the response of a lizard to tropical seasonality. *Ecology* **56:** 1243–1261.

GLOR, R. E., A. LARSON, AND J. B. LOSOS. 2005. Out of Cuba: overwater dispersal and speciation among lizards in the *Anolis carolinensis* subgroup. *Molecular Ecology* **14:** 2419–2432.

GRETHER, G. F., N. LOSIN, C. N. ANDERSON, AND K. OKAMOTO. 2009. The role of interspecific interference competition in character displacement and the evolution of competitior recognition. *Biological Reviews* **84:** 617–635.

GRONIG, J., AND A. HOCHKIRCH. 2008. Reproductive interference between species. *Quarterly Review of Biology* **83:** 257–282.

HAGMAN, M., AND R. SHINE. 2006. Spawning site selection by feral cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Austral Ecology* **31:** 551–558.

HENDRY, A. P., S. K. HUBER, L. F DE LEÓN, A. HERREL, AND J. PODOS. 2009. Disruptive selection in a bimodal population of Darwin's finches. *Proceedings of the Royal Society B* **276:** 753–759.

HESS, N. E., AND J. B. LOSOS. 1991. Interspecific aggression between *Anolis cristatellus* and *A. gundlachi*: comparisons of sympatric and allopatric populations. *Journal of Herpetology* **25:** 256–259.

HUEY, R. B., E. R. PIANKA, M. E. EGAN, AND L. W. COONS. 1974. Ecological shifts in sympatry: Kalahari fossorial lizards (*Typhlosaurus*). *Ecology* **55:** 304–316.

JENSSEN, T. A. 1973. Shift in the structural habitat of *Anolis opalinus* due to congeneric competition. *Ecology* **54:** 863–869.

JENSSEN, T. A. 1977. Evolution of anoline lizard display behavior. *American Zoologist* **17:** 203–215.

JENSSEN, T. A. 1978. Display diversity in anoline lizards and problems of interpretation, pp. 269–285. *In* N. Greenberg, and P. D. MacLean eds. *Behavior and Neurology of Lizards*. Rockville, Maryland, National Institute of Mental Health.

JENSSEN, T. A., N. GREENBERG, AND K. A. HOVDE. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and postbreeding seasons. *Herpetological Monographs* **9:** 41–62.

JENSSEN, T. A., D. L. MARCELLINI, C. A. PAGUE, AND L. A. JENSSEN. 1984. Competitive interference between the Puerto Rican lizards, *Anolis cooki* and *A. cristatellus*. *Copeia* **1984:** 853–862.

JENSSEN, T. A., AND S. C. NUNEZ. 1998. Spatial and breeding relationships of the lizard, *Anolis carolinensis*: evidence of intrasexual selection. *Behaviour* **135:** 981–1003.

JOHNSON, M. A., L. J. REVELL, AND J. B. LOSOS. 2009. Behavioral convergence and adaptive radiation: effects of habitat use on territorial behavior in *Anolis* lizards. *Evolution* **64:** 1151–1159.

KATS, L. B., AND A. SIH. 1992. Oviposition site selection and avoidance of fish by streamside salamanders (*Ambystoma barbouri*). *Copeia* **1992:** 468–473.

KOLBE, J. J., P. L. COLBERT, AND B. E. SMITH. 2008. Niche relationships and interspecific interactions in Antiguan lizard communities. *Copeia* **2008:** 261–272.

LAWTON, J. H. 1983. Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology* **28:** 23–39.

LEAL, M., AND L. J. FLEISHMANN. 2002. Evidence for habitat partitioning based on adaptation to environmental light in a pair of sympatric lizard species. *Proceedings of the Royal Society of London B* **269:** 351–359.

LEAL, M., AND L. J. FLEISHMANN. 2004. Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. *The American Naturalist* **163:** 26–39.

LISTER, B. C., AND A. G. AGUAYO. 1992. Seasonality, predation, and the behaviour of a tropical mainland anole. *Journal of Animal Ecology* **61:** 717–733.

LOSOS, J. B. 2009. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. Berkeley, University of California Press.

LOSOS, J. B., J. C. MARKS, AND T. W. SCHOENER. 1993. Habitat use and ecological interactions of an introduced and a native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes of anole introductions. *Oecologia* **95:** 525–532.

LOSOS, J. B., AND D. A. SPILLER. 1999. Differential colonization success and asymmetrical interactions between two lizard species. *Ecology* **80:** 252–258.

MEDEL, R. G., P. A. MARQUET, AND F. M. JAKSIC. 1988. Microhabitat shifts of lizards under different contexts of sympatry: a case study with South American *Liolaemus*. *Oecologia* **76:** 567–569.

NUNEZ, S. C., T. A. JENSSEN, AND K. ERSLAND. 1997. Female activity profile of a polygynous lizard (*Anolis carolinensis*): evidence of intersexual asymmetry. *Behaviour* **134:** 205–223.

ORD, T. J., AND E. P. MARTINS. 2006. Tracing the origins of signal diversity in anole lizards: phylogenetic approaches to inferring the evolution of complex behaviour. *Animal Behaviour* **71:** 1411–1429.

ORD, T. J., R. A. PETERS, B. CLUCAS, AND J. A. STAMPS. 2007. Lizards speed up visual display in noisy motion environments. *Proceedings of the Royal Society of London B* **264:** 1057–1062.

Paterson, A. V. 1999. Effects of prey availability on perch height of female bark anoles, *Anolis distichus*. *Herpetologica* **55:** 242–247.

Perry, G. 1996. The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behaviour and diet. *Canadian Journal of Zoology* **74:** 1238–1425.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20:** 297–330.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rand, A. S. 1964. Ecological distribution in anoline lizards of Puerto Rico. *Ecology* **45:** 745–752.

Reagan, D. P. 1992. Congeneric species distribution and abundance in a three-dimensional habitat: the rainforest anoles of Puerto Rico. *Copeia* **1992:** 392–403.

Schluter, D., and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. *American Naturalist* **140:** 85–108.

Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49:** 704–726.

Schoener, T. W. 1975. Presence and absence of habitat shift in some widespread lizard species. *Ecological Monographs* **45:** 233–258.

Schröder, M. S., A. C. Culhane, J. Quackenbush, and B. Haibe-Kains. 2011. *survcomp*: an R/Bioconductor package for performance assessment and comparison of survival models. *Bioinformatics* **27:** 3206–3208.

Singhal, S., M. A. Johnson, and J. T. Ladner. 2007. The behavioral ecology of sleep: natural sleeping site choice in three *Anolis* lizard species. *Behaviour* **144:** 1033–1052.

Stamps, J. A., and D. P. Crews. 1976. Seasonal changes in reproduction and social behaviour in the lizard *Anolis aeneus*. *Copeia* **1976:** 467–476.

Thornton, A., and S. J. Hodge. 2009. The development of foraging microhabitat preferences in meerkats. *Behavioral Ecology* **20:** 103–110.

Wanless, S., D. Gremillet, and M. P. Harris. 1998. Foraging activity and performance of Shags *Phalacrocax aristotelis* in relation to environmental characteristics. *Journal of Avian Ecology* **29:** 49–54.

Whitlock, M. C. 2005. Combining probability from independent tests: the weighted *Z*-method is superior to Fisher's approach. *Journal of Evolutionary Biology* **18:** 1368–1373.

Williams, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Quarterly Review of Biology* **44:** 345–389.